

# GEOGRAPHIC AND ECOLOGICAL VARIATION IN THE FAMILY ICTERIDAE

PETER E. LOWTHER

The passerine family Icteridae, restricted to but ranging throughout the New World, includes oropendolas, caciques, orioles, blackbirds, meadowlarks, grackles, and cowbirds. The family comprises 95 species placed in 23 genera (Blake 1968; Short 1968, 1969). Comparison of various aspects of the biology of members of such a diverse group may suggest patterns in the evolution of ecological adaptations. These patterns, in turn, may facilitate an analysis of part of the mechanism of adaptive radiation. In this paper I examine variation in size, ecological requirements, breeding biology, and behavior within the Icteridae and suggest explanations for the trends and relationships observed.

## METHODS

Aspects of the distribution and biology of all species were determined from the literature, insofar as it was possible, and a list of the 95 species and their attributes is given in Appendix 1. Species density was found by laying a grid with squares representing 259,000 km<sup>2</sup> over maps of species' breeding distributions and finding the number of species occurring within each grid square. After this, geographic distribution of species was simplified for analysis by considering only their latitudinal distribution, for which 30 latitude-sectors were used. These latitude-sectors are 4.64° latitude in width, the same as the north-south side of the 259,000 km<sup>2</sup> grid.

General vegetation types are influenced greatly by climate, and climates, because of the angle of solar radiation to the earth's surface and stable atmospheric circulation, have regular distributions. Particularly, North and South America have, in a general way, similar climates and vegetation types at equal distances from the equator (Fig. 1). Because of this "symmetry" of climate and vegetation about the equator, for statistical tests I combined those species occurring in latitude-sectors equal distances from the equator, on the assumption that they would be influenced by similar environmental pressures.

Statistical analyses used in this paper were 2 × 2 contingency tables, to test associations, and rank correlations, to test for trends with latitude and range size. A description of these statistical methods and appropriate tables can be found in Conover (1971).

The following "definitions" were used in categorizing species:

*Latitude*.—Species are either "tropical" (center of range within 20° of the equator) or "temperate" (center of range farther than 20° from the equator).

*Habitat preference*.—Preferred breeding habitat of each species may be "forest", "edge", "scrub", "grassland", "marsh", or "island". *Forest* is used to indicate species of the forest interior. *Edge* indicates species described as inhabiting "open woods", "forest borders", "thickets", "brushy second growth", and "ecotones" or "edges". *Scrub* refers to birds of the more arid edge habitats. *Grasslands* includes birds of the prairie

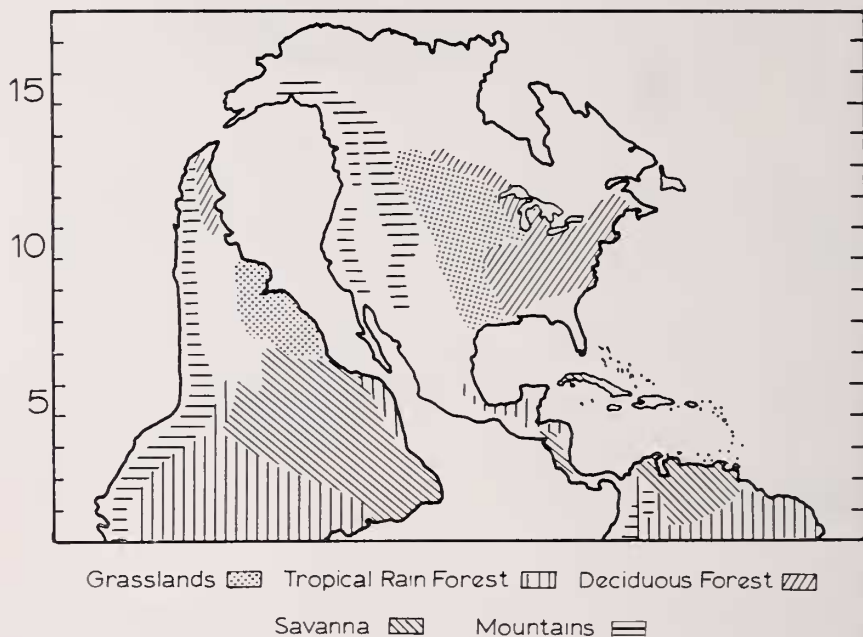


FIG. 1. Distribution of certain vegetation types. This presentation is used to emphasize that similar vegetation types occur equal distances from the equator. East is to the right. Latitude-sectors are indicated on the left. Vegetation distribution is after Kùchler (1960).

and pampas regions, "fields", "pastures", and other open grassy habitats. *Marsh* indicates species nesting primarily in marsh and marsh-like habitats. *Island* is used to indicate those species restricted to islands of the West Indies. These habitat classes are also lumped into "woods"—including forest, edge, and scrub habitats—and "open" habitats—being comprised of grasslands and marsh.

*Migratory behavior.*—A species is "migratory" if it migrates either completely (the winter or non-breeding distribution overlapping little, if any, with its breeding distribution), or only partially (the winter distribution contained within the breeding range, but populations of higher latitudes moving to regions closer to the equator). "Non-migrants" show no north-south seasonal change in distribution. In some non-migrants there may be localized movements, such as altitudinal changes, but this is not migration.

*Sexual dimorphism.*—Sexual size dimorphism is arbitrarily a difference in wing length between males and females of at least 10%. Sexual plumage dimorphism refers to noticeable plumage differences between sexes as indicated by field guide descriptions. I consider species to be sexually monomorphic if neither of these criteria are met.

*Mating system.*—Mating systems are monogamous or non-monogamous. Monogamous

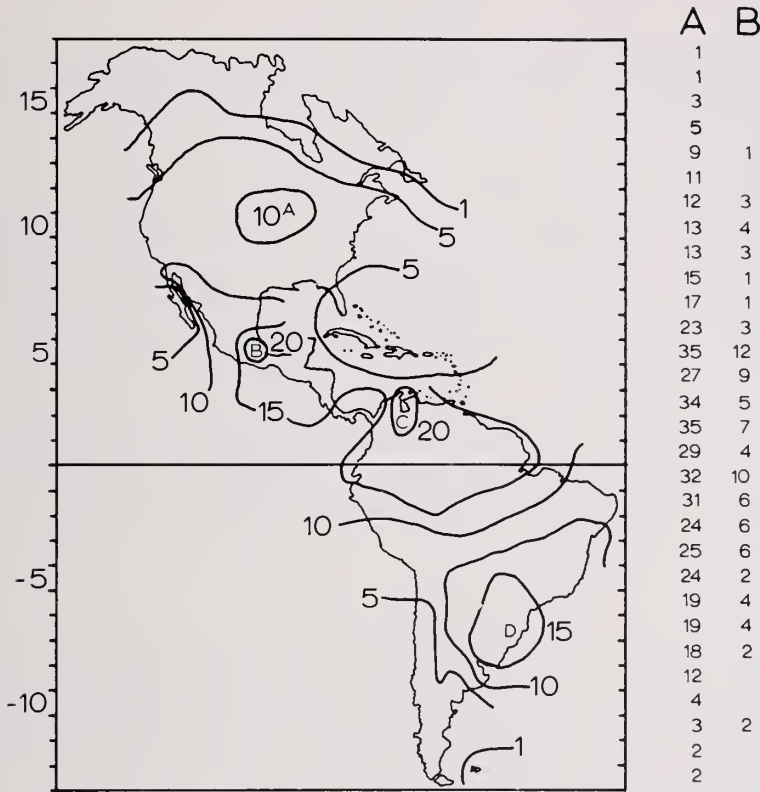


FIG. 2. Species density for breeding distribution of icterids. Isopleths are shown for 1, 5, 10, and 20 species. The 4 regions of greater density are represented as follows: A—midwestern U.S. (10 species); B—Oaxaca, Mexico (20 species); C—northwestern Venezuela (23 species); and D—Uruguay (18 species). Latitude sectors are indicated on the right.

Column A gives the total number of species occurring within the associated latitude sector. Column B gives the number of species whose center of range is included in that sector.

species are those in which a male pairs with a single female for a nesting attempt. Non-monogamous mating systems include those described as polygamous and polybrachygamous ("promiscuous"). In these cases the male has pair bonds with more than one female during a breeding attempt (see Selander 1972:193).

*Territory type.*—Territory type, or nesting dispersion, is either Type A or Type O. The first is shown by solitary nesting species. Territories of these species are breeding-nesting-feeding territories (type A) of Nice (1943). The second is shown by those colonial nesting species or those with grouped territories. For these species, territories are nesting only (type D) or nesting-breeding (type B) as categorized by Nice.

## SPECIES DENSITY

There are 4 regions where species of Icteridae show relatively greater diversity (Fig. 2): midwestern United States, southern Mexico (Oaxaca), northwestern Venezuela, and the region about Uruguay: Beecher (1950) considered this last region to be the center of icterid origins. One association between species density and general vegetation appears obvious. The midwestern U.S. and Uruguay regions are predominantly grassland habitats. The midwestern U.S. is also an area where several icterids are presently expanding their range (Bobolink, *Dolichonyx oryzivorus*; Western Meadowlark, *Sturnella neglecta*; Brewer's Blackbird, *Euphagus cyanocephalus*; Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*; and Brown-headed Cowbird, *Molothrus ater*; De Vos 1964, Mayfield 1965, and Stepney and Power 1973). These are grassland or edge species that are assumed to be expanding their range because the clearing of forested areas for agricultural purposes has increased suitable habitat for them. The other 2 areas of high species abundance cannot be associated with a single vegetation type since there is greater habitat diversity in the grid squares of the areas.

## LATITUDINAL TRENDS

More species occur in the tropics than in temperate regions, a pattern that is obviously not related to continental land area (see Fig. 2). While increased diversity in the tropics has been observed for various groups of organisms (e.g., birds, Cook 1969, Tramer 1974; mammals, Simpson 1964, Wilson 1974; reptiles and amphibians, Kiester 1971), no single causal explanation has been generally accepted. One hypothesis is that, since the tropics have had relatively stable environmental conditions for long periods of time, many species were able to evolve. MacArthur and MacArthur (1961) and Tramer (1969) have shown that bird species diversity increases with increasing complexity of vegetation structure, which is true as the tropics are approached. Ricklefs (1973) also indicates that this increase in avian diversity is related to environmental complexity rather than productivity. Thus, the high density of species in midwestern U.S. and Uruguay regions is probably caused by a mosaic of grassland-deciduous forest; the species density in the Oaxaca and Venezuela regions is a result of greater vegetation complexity superimposed on a heterogeneous topography.

*Migration.*—In seasonal environments, one would expect a greater proportion of migratory species than in non-seasonal environments. It is expected, then, that those species occurring farther from the equator (i.e., those in more seasonal environments) are more likely to be migratory. The very highly significant rank correlation between distance from the equator

TABLE I

RANK CORRELATION COEFFICIENTS BETWEEN LATITUDE AND POLYTYPOISM, LATITUDE AND MIGRATORY BEHAVIOR, AND LATITUDE AND SEXUAL DIMORPHISM

	Rank Correlation	T	Probability
Distance from equator for center of species' range			
Polytypism	0.1818	0.5847	.9 > p > .5
Migratory Behavior	0.9598	10.8134	p < .001
Sexual Dimorphism: Size	-0.6748	2.8917	p < .05
Plumage	0.9353	8.3595	p < .001
Either	0.4930	1.7919	.2 > p > .1
Distance from equator for whole of species' occurrence			
Sexual Dimorphism: Size	-0.3070	1.2493	.4 > p > .2
Plumage	0.9816	19.9195	p < .001
Either	-0.3883	1.0981	.4 > p > .2

and the proportion of migratory species supports this commonly made observation (see Table I).

*Sexual dimorphism.*—No association was found between secondary sexual size and plumage dimorphism ( $\chi^2 = 0.009$ ,  $.975 > p > .9$ ). Each form of sexual dimorphism will therefore be considered separately.

*Sexual dimorphism in size.*—There is a significant negative rank correlation between the proportion of species that are sexually dimorphic in size and the distance species occur from the equator (Table I). This trend is also indicated when the data are tested in a  $2 \times 2$  contingency table ( $\chi^2 = 9.97$ ,  $p < .001$ ).

Selander (1966) has suggested that where interspecific competition exists, sexual dimorphism in size often is not observed, but with less intense interspecific competition pressure, size dimorphism between the sexes is of greater selective advantage and is associated with differential niche use. Thus, size dimorphism is more likely when intersexual competition is of greater energetic consequence. Such a situation may apply to colonial species, since many individuals of a single species live in a relatively restricted area. If this is true, then breeding dispersion may be important in explaining the relationship between latitude and size dimorphism because colonial species (Type O territories), show size dimorphism ( $\chi^2 = 21.58$ ,  $p < .001$ ), and tend to be tropical ( $\chi^2 = 5.35$ ,  $p < .05$ ).

*Sexual dimorphism in plumage.*—A highly significant positive rank correlation exists between latitude and the proportion of species showing

plumage dimorphism (Table 1). That is, there is a greater occurrence of plumage dimorphism toward the higher latitudes. Hamilton (1961)—comparing tropical and North American *Icterus*—provided an hypothesis to explain this trend. He noted that those species farthest from the equator were generally migratory and were also frequently dimorphic in plumage. Since males show intense agonistic behavior during the breeding season, females resembling males would cause increased intersexual aggression and result in longer time required for pair formation. Migratory temperate species have a relatively shorter breeding season than tropical species and as a result, Hamilton expected plumage dimorphism to be important in reducing agonistic encounters between male and female and to shorten the time required for pair formation. I tested for association between migratory behavior and plumage dimorphism and confirmed that migratory species do tend to be sexually dimorphic in plumage ( $\chi^2 = 12.24$ ,  $p < .001$ ).

#### ECOLOGICAL TRENDS

*Sexual dimorphism in relation to habitat.*—With 5 habitat classes the association between sexual dimorphism and habitat preference is significant for both size dimorphism ( $\chi^2 = 11.38$ ,  $p < .05$ ,  $df = 4$ ) and plumage dimorphism ( $\chi^2 = 16.28$ ,  $p < .01$ ,  $df = 4$ ). Here 3 observations are noteworthy: (1) size dimorphism between the sexes occurs more frequently in forest species; (2) forest species do not show expected frequency of plumage dimorphism; and (3) marsh species tend to show plumage dimorphism. This is partly an artifact of the classification used here—those species classified as forest birds were also restricted to the tropics. When categories were lumped to produce “woods” and “open” habitat sets, I found no association between size dimorphism and habitat ( $\chi^2 = 1.78$ ,  $.5 > p > .1$ ), but there was a significant association between plumage dimorphism and habitat ( $\chi^2 = 9.36$ ,  $p < .001$ ). This association may be partly related to increased visual importance of male display in territorial and reproductive behavior. Among North American icterids, the “song spread” display of several open habitat and edge species has a striking visual component associated with territorial song (see Nero 1963). The orioles, *Icterus* sp., which inhabit more wooded environments, do not have such well developed displays accompanying their song (Skutch 1954, Bent 1958). These displays can be seen from greater distances in exposed habitats and are more appropriate for open habitats in a functional sense.

*Mating systems and territory type.*—Selander (1972) points out that sexual dimorphism in size is frequently associated with non-monogamous mating systems. I found this to be true for the Icteridae ( $\chi^2 = 23.88$ ,  $p < .001$ ). Selander discusses this further in terms of sexual selection with

size dimorphism being one consequence. In polygamous species there is increased sexual selection among males to show greater dominance (= fitness) and to mate with females. This competition for optimum territories and for females is accomplished through dominance established by larger size in males. Icterid displays often emphasize size by ruffling body feathers (e.g., "song spread"). Colonial species are also likely to be sexually dimorphic in size ( $\chi^2 = 21.58$ ,  $p < .001$ ). Mating systems and territory type are themselves significantly associated ( $\chi^2 = 21.36$ ,  $p < .001$ )—colonial species tend to be non-monogamous.

I did not find that polygamy is associated with open habitats ( $\chi^2 = 1.99$ ,  $.5 > p > .1$ ), as Verner and Willson (1966) concluded, but their habitat classification differed from mine. In their view, polygamy can evolve if a female that mates with an already mated male with a territory of good quality has an advantage over one mating with an unmated male occupying poorer quality territory. Orians (1969) further developed this model. In marshes, where many polygamous icterids breed, productivity distribution is highly variable, a factor that is considered an important prerequisite for the development of polygamy.

#### TRENDS RELATED TO RANGE SIZE

*Polytypism.*—There seems to be no pattern in the latitudinal distribution of polytypic species (Table 1) and I find it impossible to hypothesize about geographic characteristics favoring speciation. Comparison of the size of mean breeding ranges of polytypic and monotypic species showed that the gross breeding ranges of polytypic species are about  $2\frac{1}{2}$  times larger than those of monotypic species (3,700,000 km<sup>2</sup> compared to 1,400,000 km<sup>2</sup>). Rank correlation between range size and average number of subspecies for each range size class gave a significant association ( $\rho = 0.71$ ,  $p \leq .05$ ). Using the number of named subspecies as a rough measure of the amount of differentiation within a species, I found that widely distributed species are more differentiated. There was no significant association between general habitat types and polytypism ( $\chi^2 = 3.13$ ,  $.1 > p > .05$ ).

*Other trends with range size.* In addition to that with polytypism, I found significant rank correlations for range size and occurrence of migratory behavior ( $\rho = 0.89$ ,  $p < .01$ ) and for range size and occurrence of Type O territories ( $\rho = 0.77$ ,  $p < .05$ ). The first of these should be related to latitudinal occurrence, but I found no association between latitude and range size ( $\chi^2 = 0.52$ ,  $.5 > p > .1$ ). Instead migratory behavior may be related to continental land area per latitude sector: there is greater land area per latitude sector in temperate North America where most migratory species occur. The relationships between range size and both territory

type and mating system is obscure and I can suggest no explanation for them.

#### SUMMARY AND CONCLUSIONS

Morphological variation within Icteridae (in the form of sexual dimorphism) may be best explained as results of 2 types of selection. Intersexual competition is the selective force behind sexual dimorphism in size and epigamic sexual selection is the cause of plumage dimorphism.

Neither size dimorphism nor plumage dimorphism show significant associations directly with any of the remaining 7 aspects of biology examined in this analysis except latitude. Plumage dimorphism is more common within the family at higher latitudes; size dimorphism more commonly occurs at lower latitudes. My results are in agreement with Hamilton's (1961) explanation for plumage dimorphism and also offer some support for Selander's (1966, 1972) observations on size dimorphism.

#### ACKNOWLEDGMENTS

I would like to thank especially Professor R. F. Johnston for his encouragement, helpful discussions and criticisms throughout the development of this paper. At various stages the following people have read, discussed and offered helpful criticism of the paper: Drs. R. S. Hoffmann, N. A. Slade, and R. M. Mengel; also C. L. Cink, K. S. Harris, J. W. Koeppl, D. M. Mortimer, E. C. Murphy, J. W. Parker, and J. D. Robins. For all of this aid I am greatly appreciative.

#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds, 5th ed. AOU, Baltimore.
- BEECHER, W. J. 1950. Convergent evolution in the American orioles. *Wilson Bull.* 62:50-86.
- BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. *U. S. Natl. Mus. Bull.* 211.
- BLAKE, E. R. 1968. Family Icteridae, pp. 138-202. *In* Checklist of birds of the world vol. 14, (R. A. Paynter, ed.). *Mus. Comp. Zool., Cambridge, Mass.*
- BOND, J. 1971. *Birds of the West Indies*, 2nd ed. Houghton Mifflin Co., Boston.
- CONOVER, W. J. 1971. *Practical nonparametric statistics*. John Wiley and Sons, New York.
- COOK, R. E. 1969. Variation in species density of North American birds. *Syst. Zool.* 18:63-84.
- DAVIS, L. I. 1972. *A field guide to the birds of Mexico and Central America*. Univ. Texas Press, Austin.
- De Vos, A. 1964. Range changes of birds in the Great Lake region. *Am. Midl. Nat.* 71:489-502.
- EDWARDS, E. P. 1972. *A field guide to the birds of Mexico*. E. P. Edwards, Sweet Briar, Va.
- ERSKINE, A. J. 1971. Some new perspectives on the breeding ecology of Common Grackles. *Wilson Bull.* 83:352-370.



- FFRENCH, R. 1973. A guide to the birds of Trinidad and Tobago. Livingston Publ. Co., Wynnewood, Pa.
- FRIEDMANN, H. 1929. The cowbirds. Charles Thomas Publ., Springfield, Ill.
- HAMILTON, T. H. 1961. On the function and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. *Am. Nat.* 95:121-123.
- KARR, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* 41:207-233.
- KIESTER, A. R. 1971. Species density of North American amphibians and reptiles. *Syst. Zool.* 20:127-137.
- KÜCHLER, A. W. 1960. Natural vegetation [map]. In *Goode's world atlas*, 11th ed. (E. B. Espenshade, ed.). Rand McNally and Co., Chicago.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., Ltd., London.
- MACARTHUR, R. H. AND J. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594-598.
- MAYFIELD, H. 1965. The Brown-headed Cowbird, with old and new hosts. *Living Bird* 4:13-28.
- MEYER DE SCHAUENSEE, R. 1964. The birds of Columbia. Livingston Publ. Co., Narberth, Pa.
- . 1966. The species of birds of South America and their distribution. Livingston Publ. Co., Narberth, Pa.
- . 1970. A guide to the birds of South America. Livingston Publ. Co., Wynnewood, Pa.
- MONROE, B. L., JR. 1968. A distributional survey of the birds of Honduras. *Ornithol. Monogr.* No. 7.
- NERO, R. W. 1963. Comparative behavior of the Yellow-headed Blackbird, Red-winged Blackbird, and other icterids. *Wilson Bull.* 75:376-413.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow. II. The behavior of the Song Sparrow and other passerines. *Trans. Linn. Soc. N. Y.* 6:1-328.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589-603.
- . 1972. The adaptive significance of mating systems in the Icteridae, p. 389-398. In *Proc. 15th Int. Ornithol. Congr.* (K. H. Voous, ed.). E. J. Brill, Leiden.
- PARKES, K. C. 1966. Geographic variation in Azara's Marsh Blackbird, *Agelaius cyanopus*. *Proc. Biol. Soc. Wash.* 79:1-12.
- . 1970. A revision of the Red-rumped Cacique *Cacicus haemorrhous* (Aves: Icteridae). *Proc. Biol. Soc. Wash.* 83:203-214.
- PETERSON, R. T. AND E. L. CHALIF. 1973. A field guide to Mexican birds and adjacent Central America. Houghton Mifflin Co., Boston.
- PHELPS, W. H., JR. AND R. AVELEDO H. 1966. A new subspecies of *Icterus icterus* and other notes on the birds of northern South America. *Am. Mus. Novit.* 2270.
- RICKLEFS, R. E. 1973. *Ecology*. Chiron Press, Newton, Mass.
- RIDGWAY, R. 1902. The birds of North and Middle America. Part II. *U. S. Natl. Mus. Bull.* 50.
- ROBBINS, C. S., B. BRUUN, H. S. ZIM, AND A. SINGER. 1966. *Birds of North America*. Golden Press, New York.
- SCLATER, P. L. 1886. Catalogue of the Passeriformes, or perching birds, in the collection of the British Museum. Vol. 11. Part II. *Br. Mus., London.*

- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- . 1972. Sexual selection and dimorphism in birds, pp. 180-230. *In* Sexual selection and the descent of man 1871-1971 (B. Campbell, ed.). Aldine Publ. Co., Chicago.
- SIMPSON, G. G. 1964. Species density of North American recent mammals. *Syst. Zool.* 13:57-73.
- SHORT, L. L., JR. 1968. Sympatry of red-breasted meadowlarks in Argentina, and the taxonomy of meadowlarks (Aves: *Leistes*, *Pezites*, and *Sturnella*). *Am. Mus. Novit.* 2349.
- . 1969. A new species of blackbird (*Agelaius*) from Peru. *Occas. Pap. Mus. Zool. La. State Univ.* 36:1-8.
- SKUTCH, A. F. 1954. Life histories of Central American birds. *Pac. Coast Avifauna*, No. 31.
- . 1972. Studies of tropical American birds. *Publ. Nuttall Ornithol. Club*, No. 10.
- STEPNEY, P. H. R. AND D. M. POWER. 1973. Analysis of the eastern breeding expansion of Brewer's Blackbird plus general aspects of avian expansions. *Wilson Bull.* 85:452-464.
- TERBORGH, J. 1971. Distribution on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:23-40.
- TRAMER, E. J. 1969. Bird species diversity: Components of Shannon's formula. *Ecology* 50:927-929.
- . 1974. On latitudinal gradients in avian diversity. *Condor* 76:123-130.
- WILSON, J. W., III. 1974. Analytical zoogeography of North American mammals. *Evolution* 28:124-140.
- VERNER, J. AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. *Ecology* 47:143-147.

MUSEUM OF NATURAL HISTORY, UNIV. OF KANSAS, LAWRENCE 66045. ACCEPTED 24 JAN. 1975.

## APPENDIX I. CHARACTERISTICS OF THE ICTERIDAE

The classification follows Blake (1968) and Short (1968, 1969) where information on number of subspecies, center of range, range size, and migratory behavior were also obtained. Other sources for this information: American Ornithologists' Union (1957), Beecher (1950), Bond (1971), Friedmann (1929), Meyer de Schauensee (1966), Peterson and Chalif (1973), and Robbins et al. (1966).

Center of range is shown as the latitude-sector north (+) or south (-) of the equator in which the center of a species' breeding distribution occurs.

Range size is divided into 8 classes: 1 (very restricted; type locality only or small islands), 2 (to  $3.50 \times 10^6$  km<sup>2</sup>), 3 (to  $10.00 \times 10^6$  km<sup>2</sup>), 4 (to  $16.50 \times 10^6$  km<sup>2</sup>), 5 (to  $32.50 \times 10^6$  km<sup>2</sup>), 6 (to  $65.00 \times 10^6$  km<sup>2</sup>), 7 (to  $97.25 \times 10^6$  km<sup>2</sup>), and 8 (to  $120.00 \times 10^6$  km<sup>2</sup>). A 5+ indicates range is larger than  $25.03 \times 10^6$  km<sup>2</sup>, the mean range size. Range sizes were determined by measurements of mapped breeding distributions using a compensating polar planimeter.

Migratory behavior is indicated by M for migratory species, P for partial migrants, and n for non-migrants.

Habitats indicated are forest (F), edge (E), scrub (S), grassland (G), marsh (M), and island (I). Sources: Bond (1971), Davis (1972), De Vos (1964), Edwards (1972), Erskine (1971), French (1973), Karr (1971), Meyer de Schauensee (1964, 1970), Monroe (1968), Peterson and Chalif (1973), and Terborgh (1971).

For size dimorphism the percent that female wing length is smaller than male wing length is given. Sources: French (1973), Friedmann (1929), Parkes (1966, 1970), Phelps and Aveledo (1966), Ridgway (1902), and Sclater (1886). S is used to show size dimorphism of 10% or greater if judged by field guide descriptions to be adequate for the criterion used and wing length measurements could not be found.

Plumage dimorphism is indicated by P. No sexual dimorphism in plumage is shown by n. (Sources used are those listed above.)

Mating systems were classified as monogamous (M) or non-monogamous (P); territory type is either Type A or Type O (see text). Lack (1968) and Orians (1972) summarize and provide references for information on mating systems and territory types in Icteridae.

Column headings are (1) Species, (2) Number of subspecies, (3) Center of range, (4) Range size class, (5) Migratory behavior, (6) Habitat, (7) Plumage dimorphism, (8) Size dimorphism, (9) Mating system, and (10) Territory type.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
<i>Psarocolius</i>									
<i>oseryi</i>	1	-3	3	n	F	n	30%	-	-
<i>latirostris</i>	1	-1	3	n	F	n	35%	-	-
<i>decumanus</i>	4	-2	8	n	E	n	28%	P	O
<i>viridis</i>	1	-1	6	n	F	n	27%	-	O
<i>atrovirens</i>	1	-4	2	n	F	n	S	-	-
<i>angustifrons</i>	7	-1	5+	n	F	n	15%	P	O
<i>wagleri</i>	2	+3	4	n	E	n	29%	P	O
<i>montezuma</i>	1	+4	3	n	E	n	25%	P	O
<i>cassini</i>	1	+1	2	n	F	n	S	-	-
<i>bifasciatus</i>	1	-1	3	n	F	n	S	-	-

## APPENDIX 1. (CONTINUED)

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
<i>guatimozinus</i>	1	+2	2	n	E	n	23%	-	-
<i>yuracares</i>	2	-1	5	n	F	n	15%	-	-
<i>Cacicus</i>									
<i>cela</i>	3	-1	7	n	E	P	23%	P	O
<i>haemorrhous</i>	2	-2	7	n	E	P	22%	P	O
<i>uropygialis</i>	3	+2	4	n	F	P	12%	M	A
<i>chrysopterus</i>	1	-6	5	n	F	n	n	-	-
<i>koepckeae</i>	1	-3	1	n	F	n	n	-	-
<i>leucorhamphus</i>	2	-2	4	n	F	n	21%	-	-
<i>chrysonotus</i>	1	-4	2	n	F	n	19%	-	-
<i>sclateri</i>	1	-1	2	n	F	n	S	-	-
<i>solitarius</i>	1	-3	7	n	E	n	10%	M	-
<i>melanicterus</i>	1	+5	2	n	F	P	15%	-	-
<i>holosericeus</i>	3	+2	5	n	E	n	10%	M	A
<i>Icterus</i>									
<i>cayanensis</i>	6	-3	8	n	E	n	n	M	A
<i>chrysater</i>	4	+3	4	n	E	n	14%	M	A
<i>nigrogularis</i>	4	+2	5	n	E	n	9%	M	A
<i>leucopteryx</i>	3	+5	1	n	I	n	7%	M	A
<i>auratus</i>	1	+5	2	n	E	P	1%	M	A
<i>mesomelas</i>	4	+3	4	n	E	n	3%	M	A
<i>auricapillus</i>	1	+3	3	n	E	n	n	M	A
<i>graceannae</i>	1	-2	2	n	S	n	n	M	A
<i>xantholemus</i>	1	-1	1	n	-	n	n	M	A
<i>pectoralis</i>	2	+4	3	n	S	n	5%	M	A
<i>gularis</i>	6	+5	3	n	E	n	8%	M	A
<i>pustulatus</i>	6	+4	4	n	E	P	8%	M	A
<i>cucullatus</i>	5	+6	4	M	E	P	5%	M	A
<i>icterus</i>	6	-3	7	n	E	n	6%	M	A
<i>galbula</i>	4	+9	7	M	E	P	7%	M	A
<i>spurius</i>	3	+9	6	M	E	P	6%	M	A
<i>dominicensis</i>	6	+4	4	n	F	n	5%	M	A
<i>wagleri</i>	2	+5	4	n	E	n	7%	M	A
<i>laudabilis</i>	1	+4	1	n	I	P	0%	M	A
<i>bonana</i>	1	+4	1	n	I	n	n	M	A
<i>oberi</i>	1	+4	1	n	I	P	9%	M	A
<i>graduacauda</i>	4	+5	3	M	E	n	5%	M	A
<i>maculialatus</i>	1	+4	2	n	E	P	n	M	A
<i>parisorum</i>	1	+7	5	M	S	P	6%	M	A
<i>Nesopsar</i>									
<i>nigerrimus</i>	1	+5	2	n	I	n	5%	-	-

## APPENDIX 1. (CONTINUED)

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
<i>Xanthopsar</i>									
<i>flavus</i>	1	-7	4	n	M	P	n	-	O
<i>Gymnomystax</i>									
<i>mexicanus</i>	1	+1	6	n	E	n	n	-	-
<i>Xanthocephalus</i>									
<i>xanthocephalus</i>	1	+11	6	M	M	P	19%	P	O
<i>Agelaius</i>									
<i>xanthophthalmus</i>									
<i>thilius</i>	1	-2	1	n	M	n	14%	M	-
<i>phoeniceus</i>	23	+10	8	P	M	P	18%	P	O
<i>tricolor</i>	1	+9	2	n	M	P	12%	P	O
<i>icterocephalus</i>	2	+1	5+	n	M	P	12%	-	O
<i>humeralis</i>	1	+6	2	n	M	P	8%	-	-
<i>xanthomus</i>	2	+5	2	n	I	n	10%	M	-
<i>cyanopus</i>	4	-4	6	n	M	P	8%	-	-
<i>ruficapillus</i>	2	-4	6	n	M	P	n	-	-
<i>Sturnella</i>									
<i>militaris</i>	1	-1	6	n	G	P	9%	M	-
<i>superciliaris</i>	1	-6	6	n	G	P	n	M	-
<i>bellicosa</i>	1	-3	3	n	G	P	n	M	-
<i>dejlippii</i>	1	-8	3	n	G	P	8%	M	-
<i>loyca</i>	4	-11	4	P	G	P	n	M	-
<i>magna</i>	14	+4	8	P	G	n	10%	P	A
<i>neglecta</i>	1	+10	7	P	G	n	11%	P	A
<i>Pseudoleistes</i>									
<i>guirahuro</i>	1	-6	5	n	G	n	n	-	-
<i>virescens</i>	1	-8	3	n	G	n	n	M	-
<i>Amblyramphus</i>									
<i>holosericeus</i>	1	-7	5	n	M	n	n	-	-
<i>Hypopyrrhus</i>									
<i>pyrohypogaster</i>	1	+2	3	n	E	n	S	-	-
<i>Curaeus</i>									
<i>curaeus</i>	2	-11	4	n	E	P	n	M	-
<i>forbesi</i>	1	-4	3	n	-	P	S	-	-
<i>Gnorimopsar</i>									
<i>chopi</i>	2	-5	6	n	G	n	6%	-	-

## APPENDIX 1. (CONTINUED)

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
<i>Oreopsar</i>									
<i>bolivianus</i>	1	-5	2	n	E	n	n	-	-
<i>Lamprosar</i>									
<i>tanagrinus</i>	5	-1	5	n	E	n	S	-	-
<i>Macroagelaius</i>									
<i>subalaris</i>	2	+2	3	n	F	n	S	-	-
<i>Dives</i>									
<i>atroviolacea</i>	1	+6	2	n	I	n	6%	-	-
<i>dives</i>	3	+1	3	n	E	P	11%	M	A
<i>Quiscalus</i>									
<i>mexicanus</i>	8	+5	5+	P	E	P	20%	P	O
<i>major</i>	2	+8	3	P	E	P	22%	P	O
<i>palustris</i>	1	+5	1	n	M	P	22%	-	-
<i>nicaraguensis</i>	1	+3	1	n	M	P	22%	-	-
<i>quiscula</i>	3	+10	6	P	E	P	11%	M	O
<i>niger</i>	7	+5	2	n	I	P	14%	M	-
<i>lugubris</i>	8	+2	3	n	E	P	13%	M	O
<i>Euphagus</i>									
<i>carolinus</i>	2	+13	6	M	E	P	5%	M	A
<i>cyaenocephalus</i>	1	+11	6	P	G	P	8%	M	O
<i>Molothrus</i>									
<i>badius</i>	3	-6	5+	n	E	n	5%	M	-
<i>rufoaxillaris</i>	1	-7	5	n	E	n	6%	M	-
<i>bonariensis</i>	7	-4	8	n	G	P	12%	M	-
<i>aeneus</i>	4	+5	4	P	E	P	11%	-	-
<i>ater</i>	3	+10	7	P	E	P	10%	M	-
<i>Scaphidura</i>									
<i>oryzivora</i>	2	-2	8	n	E	P	24%	-	-
<i>Dolichonyx</i>									
<i>oryzivorus</i>	1	+11	6	M	G	P	11%	P	A

APPENDIX 2. CHI-SQUARE TESTS OF ASSOCIATION. THE  $2 \times 2$  CONTINGENCY TABLES AND CHI-SQUARE VALUES ARE PRESENTED AS THE LOWER TRIANGLE OF A SYMMETRICAL MATRIX. SIGNIFICANCE IS INDICATED FOR 1 DEGREE OF FREEDOM.

	Latitude <sup>1</sup>		Politypsism		Range Size		Habitat		Migratory Behavior		Plumage Dimorphism		Size Dimorphism		Territory Type	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
<b>Polytypism</b>																
(a) Monotypic	18	29														
(b) Polytypic	15	33														
Chi-square	0.52															
<b>Range Size</b>																
(a) Larger than mean	13	18	9	22												
(b) Smaller than mean	20	44	38	26												
Chi-square	1.05		7.69**													
<b>Habitat</b>																
(a) Open	15	10	15	10	14	11										
(b) Woods	12	47	23	36	17	42										
Chi-square	12.66***		3.13		5.57*											
<b>Migratory Behavior</b>																
(a) Migratory	11	7	5	13	12	6	7	11								
(b) Not migratory	22	55	42	35	19	58	18	48								
Chi-square	6.81**		4.18*		11.70***		0.91									
<b>Plumage Dimorphism</b>																
(a) Present	20	24	19	25	20	24	18	21	15	29						
(b) Absent	13	38	28	23	11	40	7	38	3	48						
Chi-square	4.15*		1.30		6.13*		9.36***		12.24***							
<b>Size Dimorphism</b>																
(a) Present	9	38	21	26	17	30	10	33	10	37	22	25				
(b) Absent	24	24	26	22	14	34	15	26	8	40	22	26				
Chi-square	9.97***		0.85		0.53		1.78		0.33		0.01					
<b>Territory Type</b>																
(a) Type A	6	32	11	27	8	30	10	23	10	28	17	21	7	31		
(b) Type O	8	10	6	12	11	7	7	11	6	12	13	5	15	3		
Chi-square	5.35*		0.11		8.74**		0.39		0.29		3.71		21.58***			
<b>Mating System</b>																
(a) Monogamous	15	31	18	28	13	33	9	30	10	36	24	42	12	34	28	3
(b) Non-monogamous	6	8	5	9	10	4	6	8	7	7	8	6	14	0	3	11
Chi-square	0.49		0.05		8.46**		1.99		4.22*		2.24		23.88***		21.36***	

<sup>1</sup>Latitude: (a) temperate, (b) tropical  
\* p < .05; \*\* p < .01; \*\*\* p < .001